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Emissions of biogenic volatile organic compounds from adjacent boreal fen and bog as impacted by vegetation composition

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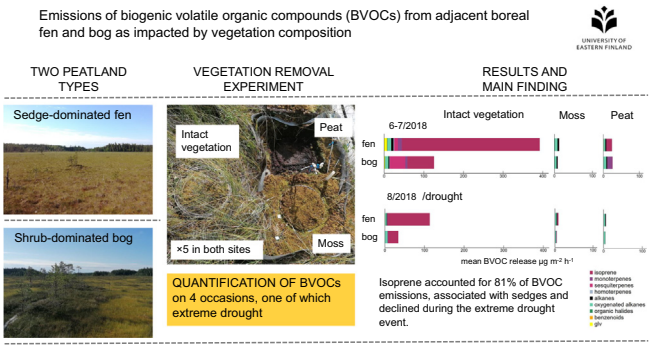
HIGHLIGHTS

- Vegetation and peat contribute to BVOC emissions in a boreal fen and bog.
- Isoprene (81 % of total) emission was associated with sedges and highest in the fen.
- Increase in shrubs may negate warming-induced increase in peatland BVOC emissions.
- Extreme drought event modified BVOC emission composition.

GRAPHICAL ABSTRACT



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ABSTRACT

Peatland ecosystems emit biogenic volatile organic compounds (BVOC), which have a net cooling impact on the climate. However, the quality and quantity of BVOC emissions, and how they are regulated by vegetation and peatland type remain poorly understood. Here we measured BVOC emissions with dynamic enclosures from two major boreal peatland types, a minerotrophic fen and an ombrotrophic bog situated in Siikaneva, southern Finland and experimentally assessed the role of vegetation by removing vascular vegetation with or without the moss layer. Our measurements from four campaigns during growing seasons in 2017 and 2018 identified emissions of 59 compounds from nine different chemical groups. Isoprene accounted for 81 % of BVOC emissions. Measurements also revealed uptake of dichloromethane. Total BVOC emissions and the emissions of isoprene, monoterpenoids, sesquiterpenes, homoterpenes, and green leaf volatiles were tightly connected to vascular plants. Isoprene and sesquiterpene emissions were associated with sedges, whereas monoterpenoids and homoterpenes were associated with shrubs. Additionally, isoprene and alkane emissions were higher in the fen than in the bog and they significantly contributed to the higher BVOC emissions from intact vegetation in the fen. During an extreme drought event in 2018, emissions of organic halides were absent. Our results indicate that climate change with an increase in shrub cover and increased frequency of extreme weather events may have a negative impact on total BVOC emissions that otherwise are predicted to increase in warmer temperatures. However, these changes also accompanied a change in BVOC emission quality. As different compounds differ in their capacity to form secondary organic aerosols, the ultimate climate impact of peatland BVOC emissions may be altered.

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1. Introduction

Peatlands are characterized by their large carbon (C) store and their function as a sink of carbon dioxide and a source of methane (Strack, 2008), although their role as a source of biogenic volatile organic compounds (BVOC) is less well known. BVOCs are reactive hydrocarbons that are released into the atmosphere from natural processes, with terrestrial vegetation being the dominant source of global emissions releasing 700–1000 Tg (10^{12}) C yr^{-1} (Guenther et al., 1995; Laothawornkitkul et al., 2009). Following their oxidation in the atmosphere, they contribute to the formation of tropospheric ozone (Atkinson, 2000) and secondary organic aerosols (SOA) (Hoffmann et al., 1997). Most aerosols cause a negative radiative forcing effect and can thus mitigate climate warming (Paasonen et al., 2013). However, BVOCs can also prolong the lifetime of the potent greenhouse gas methane in the atmosphere by competing for OH radicals (Kaplan et al., 2006). Due to these various impacts on atmospheric chemistry, it is important to understand and model BVOC dynamics in different ecosystems.

In boreal ecosystems, BVOC emissions have been quantified mostly from forests (e.g., Cleveland and Yavitt, 1998; Aaltonen et al., 2013; Mäki et al., 2017; Hellén et al., 2018 and the references therein), and the BVOC-mediated cooling impact of boreal forests has been found to be important for both boreal and arctic regions (Sporre et al., 2019: Yli-Juuti et al., 2021). In spite of large (up to 28 %) cover of peatlands in the boreal region (Kauppi et al., 1997) and the major role in climate regulation through their C cycling, BVOC emissions from peatlands under the pressure of climate change (Helbig et al., 2020) are still less studied.

To date, studies show that BVOC emissions from peatlands differ qualitatively and quantitatively from boreal forest emissions. While the latter are dominated by monoterpenes (C_{10}) (Cleveland and Yavitt, 1998; Aaltonen et al., 2013; Mäki et al., 2017; Hellén et al., 2018), boreal and subarctic peatlands have been shown to be notable sources of isoprene (2-methyl-1,3-butadiene; C_5H_8) (e.g., Janson and De Serves, 1998; Haapanala et al., 2006; Tiiva et al., 2007a), while also emitting various other BVOCs (Janson and De Serves, 1998; Janson et al., 1999; Rinnan et al., 2005; Hellén et al., 2006; Faubert et al., 2010a,b; Holst et al., 2010; Lindwall et al., 2016; Seco et al., 2020; Hellén et al., 2020). Recently, Hellén et al. (2020) found that a subarctic peatland emitted more sesquiterpenes (C_{15}) than monoterpenes, while additionally acting as a substantial source of isoprene emissions. However, all the aforementioned peatland study sites have been located in boreal and subarctic minerotrophic fens, and bogs have not received much attention to date. It is known that peatland types differ from each other; ombrotrophic bogs are nutrient poor ecosystems that have lost connection to the surrounding mineral soil due to the vertical growth of the peat layer and thus receive water and nutrients only from precipitation, while fens receive additional water and nutrients from the adjacent mineral soils and groundwater. These peatland types also differ in their vegetation composition (Vitt and Wieder, 2006; Kokkonen et al., 2019) as well as in their carbon dioxide and methane dynamics (Frolking et al., 1998; Turetsky et al., 2014). Therefore, they could also be expected to differ in terms of BVOC emissions. Although Klinger et al. (1994) in a Hudson Bay lowland found indication that peatland isoprene and terpene emissions could increase along the successional gradient from fens to bogs, to date there have been no further studies to compare BVOC emissions between the two main peatland types.

The variation in peatland BVOC emissions along the successional gradient from fens to bogs (Klinger et al., 1994) and between different microhabitats (Bäckstrand et al., 2008) is likely to be connected to differences in vegetation composition, since plant species differ in the composition of the BVOC that they release (Helmig et al., 1999; Kesselmeier and Staudt, 1999; Duhl et al., 2008). Mesocosm studies show differences in BVOC emissions between the main plant functional types of boreal peatlands, i.e., dwarf shrubs, sedges and grasses (Klinger et al., 2002; Rinnan et al., 2005; Tiiva et al., 2007a, 2009; Faubert et al., 2010b). While the common peatland sedges *Eriophorum angustifolium* and *Carex rostrata* emit only isoprene in significant amounts (Ekberg et al., 2009), ericaceous dwarf shrubs, on the other hand, can release mostly monoterpenes, similar to forest vegetation (Isebrands et al., 1999; Rinnan et al., 2005). *Sphagnum* mosses, a key element of peatland vegetation, have been shown to emit isoprene (Hanson et al., 1999; Hellén et al., 2006; Tiiva et al., 2009; Ekberg et al., 2011), as well as monoterpenes, sesquiterpenes and other BVOCs (Faubert et al., 2010b). However, the roles of vascular plants and mosses have not been systematically ascertained in the field.

Aside from vascular plants and mosses, soil and decaying litter are known to release BVOCs in boreal forests and arctic tundra (Guenther et al., 2012; Aaltonen et al., 2013; Ramirez et al., 2010; Kramshøj et al., 2018). In treeless ecosystems, such as arctic tundra and open peatlands, soil emissions can even make up a significant proportion of the ecosystem scale BVOC release (Kramshøj et al., 2016, 2018; Li et al., 2020). However, studies that aim to partition the role of vegetation and peat in peatland BVOC emissions are scarce and have been conducted mainly in the laboratory (Hellén et al., 2006; Tiiva et al., 2009; Faubert et al., 2010b). Work by Tiiva et al. (2009) has shown that the peat from a boreal bog contributes <10 % to total isoprene emission from dry hummock and wet hollow microcosms. When studying the same microcosms, Faubert et al. (2010b) found that the peat released different mixtures of BVOCs compared to the vegetation. Since these two studies are based only on bog microcosms, more research is needed to quantify the contribution of the meters-deep peat columns to BVOCs released from fen and bog ecosystems.

The aim of this study was to quantify BVOC emissions from a boreal fen and bog and to distinguish how the various plants and the peat contribute to these emissions. We expected BVOC emissions to 1) differ qualitatively and quantitatively between the fen and bog ecosystems dominated by sedges and dwarf shrubs, 2) be related to the vegetation composition, and 3) be impacted by environmental conditions: temperature, light, and water level. To address the aims of the study, we carried out removal treatments of vascular plants and mosses in two sites located within the same peatland complex, and conducted four measurement campaigns with dynamic enclosures under a range of environmental conditions. As our measurements covered an exceptionally warm and dry period during the growing season in 2018, we were also able to investigate the impact of this extreme climatic event on BVOC emissions.

2. Materials and methods

2.1. Site description

The study was conducted in a minerotrophic fen and an ombrotrophic bog that are part of the Siikaneva peatland complex situated in southern Finland (61°50′ N; 24°12′ E) (Fig. S1), 160 m a.s.l., within the southern boreal vegetation zone (Ahti et al., 1968). Annual rainfall in the area is 707 mm, snow depth in March (the month with the thickest snow cover) is 36 cm, annual cumulative temperature is 1318 degree days (based on temperatures above 5 °C), the length of the growing season is 168 days, average annual air temperature is 4.2 °C and the average air temperatures in January and July are −7.2 °C and 17.1 °C, respectively (30-year averages from the nearby Juupajoki-Hyytiälä weather station, snow depth is the 20-year average).

2.2. Experimental design

To quantify the contribution of vascular plants, mosses, and the underlying peat to total BVOC emissions, we established five clusters of study plots with vegetation removal treatments in the fen and bog sites in 2016, one year before the first BVOC measurements (see a scheme of the experimental design in Supplementary Fig. S1). The study plots were selected to represent the most characteristic vegetation community type in a fen and a bog: i.e., lawn vegetation dominated by the sedges (*Carex lasiocarpa* and *C. rostrata*) in the fen, and hummocks dominated by dwarf shrubs in the bog (Table 1). Each cluster consisted of a plot with intact vegetation (Vascular plants + Moss + Peat = VMP), a moss plot where vascular plants were removed by clipping (Moss + Peat = MP), and a bare peat

Table 1
Mean cover (%) and standard error (SE) per vascular plant and moss species in the study plots in Siikaneva fen and bog.

Species	Cover (SE)	
	Fen	Bog
Andromeda polifolia	6.8 (3.3)	0.9 (0.8)
Betula nana	3.1 (1.5)	1.2 (0.8)
Calluna vulgaris		11.8 (5.4)
Carex lasiocarpa	7.4 (2.9)	
Carex pauciflora	0.1 (0.1)	0.04 (0.0)
Carex rostrata	8.2 (3.7)	
Drosera spp.	0.44 (0.2)	0.26 (0.1)
Empetrum nigrum		2.3 (1.0)
Eriophorum vaginatum	2 (2.0)	2.6 (1.4)
Ledum palustre		0.1 (0.1)
Menyanthes trifoliata	3.4 (2.1)	
Pinus sylvestris[a]		0.04 (0.02)
Rubus chamaemorus		6.4 (1.6)
Vaccinium oxycoccos	1.6 (0.7)	9.9 (4.8)
Moss total	94.8 (1.5)	97.4 (1.1)
Sphagnum recurvum col.	38.4 (21.3)	11.6 (4.2)
S. fuscum		66.2 (17.1)
S. magellanicum[b]	8.6 (8.4)	
S. papillosum	47.8 (20.2)	
S. rubellum		19.4 (19.4)
Pleurozium schreberi		0.2 (0.2)
Polytrichum strictum	0.1 (0.1)	

[a] *P. sylvestris* germinant.
[b] Recently divided into two separate species *S. divinum* Flatberg & K. Hassel and *S. medium* Limpr.

surface (Peat = P) where both vascular plants and mosses were removed. Roots were excluded from the MP and P plots with a polypropene root barrier fabric installed to a 70 cm depth around the plots. The fabric inhibited root growth but allowed normal water flow in the plots. All vascular plants growing inside the MP and P plots were clipped whenever new growing plants were found, but in all cases, clipping was carried out at least two days before the BVOC measurements. To mimic ambient conditions in the P plots, a living moss layer was maintained over the peat surface between the measurements, which was achieved by cutting the moss carpet and placing it on a framed mesh fabric that allowed the moss layer to be lifted aside for the BVOC measurements.

2.3. BVOC measurements

We measured BVOC (C_5-C_{16}) emissions a total of four times during the growing seasons in 2017 and 2018 (referred to as campaigns). Measurements were conducted between 18th–24th July 2017 (7/2017 campaign), 27th June–8th July 2018 (6–7/2018 campaign), 21st–27th August 2018 (8/2018 campaign), and 22nd–26th October 2018 (10/2018 campaign). The last campaign represented shoulder season, when already majority of leaves were senesced in the fen, while the shrub-dominated bog was still characterized with leaves. Due to logistical reasons, measurements in the fen and bog were conducted after each other.

We used the dynamic chamber method to measure BVOC emissions (Tiiva et al., 2009; Faubert et al., 2010b; Mäki et al., 2017). For measurements, a glass chamber was placed on round stainless-steel collars (21.9 cm diameter; chamber height 40 cm) that were located at each sample plot. Incoming and outgoing air of the chamber was sampled for 1 h 45 min–2 h by pumping the air through Tenax TA-Carbopack B adsorbent tubes at a flow rate of 0.15 l min^{-1}. Ambient air was filtered through an active carbon trap and a MnO_2-coated copper net for removal of VOCs and ozone and pumped continuously into the chamber at a flow rate of 1 l min^{-1} to keep the chamber overpressurized and to prevent ingress air from the outside. The chamber air volume was flushed with filtered air for 20 min before each sampling to stabilize the system. Temperature inside the chamber was measured using a thermometer (Fluke 54II, Fluke, WA, USA). To make sure that no artifacts or contamination were considered as BVOC emissions/uptake, two blank adsorbent tubes were brought to the field on each field visit and analyzed for BVOC composition together with the samples.

2.4. Ancillary measurements

During all BVOC measurements, we recorded the height of the water table (WT) in perforated plastic tubes (2 cm diameter) installed into the peat next to each study plot cluster. Data for photosynthetically active radiation (PAR; wavelength range 400–700 nm) during each BVOC-measurement was acquired from the Siikaneva ICOS station in the fen site where it was measured with Li-Cor Li-190R quantum sensor.

A vegetation inventory of each plot was conducted in 2016 prior to the vegetation removal treatments and again in 2018 for the VMP plots (Table 1). Leaf area index (LAI) of the vascular plants growing in the VMP plots was monitored throughout both growing seasons. An estimate for an average number of leaves per square meter of area for each vascular plant species was taken from the leaf count that was conducted every third week from inside the VMP plots. Corresponding samples of each plant species were then collected from outside the study plots on each leaf area measurement day, and the number and area of the green leaves of the samples were measured in a laboratory using a leaf scanner. Area based LAI of each vascular plant species was then calculated by multiplying leaf number with average leaf size. Total LAI (LAI_{TOT}), as well as LAI of shrubs, half shrubs, sedges, and herbs for each sample plot was calculated based on the leaf area of the species growing on each site. In the fen site, LAI_{shrub} consisted of *Andromeda polifolia*, *Betula nana* and *Vaccinium oxycoccos*, LAI_{sedge} consisted of *C. lasiocarpa*, *Carex pauciflora*, *C. rostrata*, and *Eriophorum vaginatum*, and LAI_{herb} consisted of *Drosera rotundifolia*, *Menyanthes trifoliata* and *Scheuchzeria palustris*. In the bog site, LAI_{shrub} included *A. polifolia*, *B. nana*, *Calluna vulgaris*, *Empetrum nigrum*, *Rhododendron tomentosum*, *Pinus sylvestris* and *V. oxycoccos*, while $LAI_{halfshrub}$ consisted only of *Rubus chamaemorus*, LAI_{sedge} of *C. pauciflora* and *E. vaginatum*, and LAI_{herb} of *D. rotundifolia*.

2.5. BVOC sample analyses and flux calculations

The sample tubes were kept at 5 °C until they were analyzed with a thermodesorption instrument connected to a gas chromatograph. The samples collected in 2017 were analyzed in Finnish Meteorological Institute in Helsinki as described by Mäki et al. (2017). The samples collected in 2018 were analyzed in University of Eastern Finland (Kuopio) using a Perkin-Elmer ATD400 Automatic Thermal Desorption system (USA) that was connected to a Hewlett-Packard GC 6890 (Germany) gas chromatograph with a HP-5MS (60 m, 0.25 mm, 0.25 μm) column and a mass selective detector (Hewlett-Packard MSD 5973, USA). The sample tubes were thermally desorbed for 10 min at 280 °C, and were then cryofocused in a Tenax TA cold trap at −30 °C before injection into the column using rapid heating (300 °C). For the 6–7/2018 campaign samples, the column was first heated from 40 °C to 210 °C at a rate of 5 °C min^{-1} and then at a rate of 20 °C min^{-1} up to 250 °C, where it was maintained for 5 min. Total running time of the analysis was 43 min. As we expected less amounts of compounds in the 8/2018 and 10/2018 campaigns, the method was adjusted for these analyses. First, the column was heated from 40 °C to 125 °C at a rate of 5 °C min^{-1} and then at a rate of 10 °C min^{-1} up to 260 °C, where it was maintained for 3.5 min. Total running time of these analyses was 35 min. For the three 2018 sample sets, four standards in methanol solution were used for calibration by injecting them into sample tubes. The amounts injected were 2 μl of terpenoid, green leaf volatiles (GLV and HC48 indoor air standards, and 3 μl of isoprene standard, except for the analysis of the third sample set where 2 μl of the isoprene standard was injected into the tubes. All standards other than for isoprene are mixes to analyze several compounds at once. The terpenoid standard used in this study consists of 23 compounds, the GLV standard of 10 compounds and the HC48 indoor air standard includes 47 different compounds. Methanol was flushed away from the Tenax TA and Carbopack B adsorbent tubes using nitrogen (N_2) at a flow rate of 100 ml min^{-1} for 1 min.

Due to differences in the methods and instruments between the years, we report emissions of isoprene, monoterpenoids (that includes both monoterpenes and oxygenated monoterpenes) and sesquiterpenes on all four measurement occasions. The emissions of other BVOC compound groups were only inspected in 2018. The different approaches in 2017 and 2018 did not substantially alter the composition of monoterpenoid and sesquiterpene fluxes: 8/15 monoterpenoid compounds and 4/8 sesquiterpene compounds were detected in both years, composing 93 % of total monoterpenoid and 92 % of total sesquiterpene fluxes on mass-basis. Therefore, we were confident to include both years in the same analysis.

Flux rates (E, μg m^{-2} h^{-1}) of the compounds were calculated for the area inside the collar (m^2) and time (h) using Eq. (1).

$$E = (C_{out} - C_{in})\, F_{chamber} \times 60/A \quad (1)$$

where C_{in} is the concentration of ingoing air sample (μg m^{-3}) and C_{out} is the concentration of the outgoing air sample (μg m^{-3}), $F_{chamber}$ (m^3 min^{-1}) is the flow rate of air pumped into the chamber, and A (m^2) is the soil surface area inside the collar.

Detected BVOC were classified into nine groups based on their chemistry and function following the approach described in Guenther et al. (2012). The nine groups were: isoprene (hemiterpenes), monoterpenoids, sesquiterpenes, homoterpenes, alkanes, oxygenated alkanes, organic halides, benzenoids, and GLV. Negative net fluxes indicating BVOC uptake were separated from the emission data and analyzed separately.

2.6. Statistical analyses

Statistical analyses were conducted using R version 4.0.2 and data were visualized with package *ggplot2* (v 3.3.3). To test for the impact of campaign, site, treatment, and their interactions on total BVOC emissions, BVOC uptake and environmental conditions (WT, temperature, PAR and LAI), linear mixed models (package *nlme* v3.1-148; Pinheiro et al., 2014) were used. To further inspect the quality of BVOC emissions, the *lmes* were followed by multivariate generalized linear models (package *mvabund* v4.1.9; Wang et al., 2012) that tested the effect of measurement campaign, site, treatment (VMP/MP/P) and their interactions on BVOC compounds and BVOC group emissions. For BVOC group emissions, we included data from both years (2017 and 2018) considering homoterpenes, alkanes, oxygenated alkanes, organic halides, benzenoids, and GLVs in 2017 as missing values. For BVOC compounds, only data from 2018 was used. Compounds that were detected only once or twice (eight compounds) were excluded from the data. In both tests, the observed BVOC emissions were logarithmically transformed as by Anderson et al. (2006), models were fitted with negative binomial distribution using 999 bootstrap iterations and reported with log-likelihood ratio statistics. The nested and repeated measured study design were accounted for by setting plot within the plot cluster as strata. To reveal differences on the individual BVOC groups and compounds, the multivariate generalized linear models were followed by univariate tests. For the compound groups p-values of the univariate test are reported unadjusted, whereas for the individual compounds, p-values were adjusted to the multiple testing, thus highlighting the compounds responding the strongest.

The variation in the composition of BVOC groups in 2017 and 2018 was further visualized using principal component analysis (PCA) using the package FactoMineR (v2.4; Lê et al., 2008) that allowed the missing data for some BVOC groups in 2017. PCAs were based on the Anderson's log-transformed emissions.

To study the relationships between total/group BVOC emissions and water level and vegetation composition, correlations between total/group emissions and WT, LAI_{TOT}, LAI_{shrub}, $LAI_{halfshrub}$, LAI_{sedge} and LAI_{herb} were calculated with the package *corrplot* (v0.90). As temperature is the main driver of BVOC emissions, its effect on the total/group emissions was first neutralized by standardizing the emissions for T = 20 °C, modified after Guenther et al. (1993). As isoprene emission is also known to be dependent on light, they were standardized for both temperature and light (T = 20 °C and PPFD = 1000 μmol m^{-2} s^{-1}) using the algorithm described in Guenther et al. (1993). For the correlation analyses Anderson's log-transformation was used again on the standardized total/group emissions. We chose to use T = 20 °C instead of T = 30 °C in the emission standardization as the former is an ecologically more relevant temperature during the growing season in the boreal zone. However, we also used the same algorithm with T = 30 °C to calculate the emission potential of isoprene for comparison with previous studies (Guenther et al., 1993; Janson and De Serves, 1998; Haapanala et al., 2006; Hellén et al., 2006; Tiiva et al., 2009; Seco et al., 2020).

3. Results

3.1. Environmental conditions

The growing season of 2018 was very warm with higher mean temperature values observed in the chamber ($T_{chamber}$) during the 6–7/2018 and 8/2018 campaigns than during the 7/2017 campaign (25 °C, 22 °C, and 18 °C, respectively, DF = 3, 64; $p < 0.0001$). The mean $T_{chamber}$ value was lowest during the shoulder season 10/2018 campaign, as was PAR compared to the other campaigns (DF = 3, 64; $p < 0.0001$). Mean $T_{chamber}$ and PAR values during our measurement campaigns did not differ between sites ($p = 0.3965$ and $p = 0.8312$) or between treatments ($p = 0.2971$ and $p = 0.1776$, respectively).

Total LAI (0.26 in the fen and 0.19 in the bog) did not significantly differ between sites (DF = 1, 8; $p = 0.1106$). Reflecting the plot selection, LAI in the bog was dominated by dwarf shrubs and half shrubs (i.e., *Rubus chamaemorus*) (effect of site on LAI_{shrub} $p = 0.0188$ and on $LAI_{halfshrub}$ $p = 0.0014$), whereas LAI in the fen was dominated by sedges (effect of site on LAI_{sedge} $p = 0.0064$) (Fig. 1). Herb LAI was low at both sites (Fig. 1) and did not differ significantly between sites ($p = 0.2804$).

Also reflecting the plot selection, the fen plots were significantly wetter than the bog plots (DF = 1, 28; $p < 0.0001$) (Fig. 1). There was a strong seasonality in WT, which differed between measurement campaigns (DF = 3, 76; $p < 0.0001$). The warm growing season in 2018 was also very dry with the lowest WT (−24 cm in the fen and −35 cm in the bog) recorded during the 8/2018 campaign (Fig. 1). In 2018, WT was highest during the autumn campaign (10/2018), when it approached the values observed in the middle of the growing season in 2017 (7/2017 campaign).

3.2. Quantity and composition of BVOC emissions

A total of 59 compounds were identified, seven of which were detected only once or twice (Table S1). Additionally, 25 compounds were detected but could not be identified and quantified with the standards available. The most abundant compound was isoprene, which generally exhibited net emission rates an order of magnitude higher than the other BVOC groups (range: 0–717.5 μg m^{-2} h^{-1}; mean 85.1 μg m^{-2} h^{-1} from intact vegetation) (Fig. 1). The emission potential of isoprene (T = 30 °C and PPFD = 1000 μmol m^{-2} s^{-1}), calculated using the algorithm presented in Guenther et al. (1993), ranged from 0 to 978.6 μg m^{-2} h^{-1} (mean: 137.4 μg m^{-2} h^{-1} from intact vegetation). Isoprene was the only hemiterpene detected and (E)-4,8-dimethyl-1,3,7-nonatriene (E-DMNT) was the only homoterpene detected.

As expected, net BVOC emission rates increased with increasing temperature (effect of $T_{chamber}$ on total BVOC emissions: DF = 1, 81; $p < 0.0001$). We found strong seasonality in BVOC emissions as campaign explained the most variation in emissions (Figs. 1 and S2, Table 2) Elevated isoprene, monoterpenoid, sesquiterpene, homoterpene, alkane, benzenoid and GLV emission rates were typical in the 6–7/2018 campaign when $T_{chamber}$, LAI_{total} and PAR were greatest (Fig. 2). In addition, oxygenated alkane emission rates were higher during the 6–7/2018 and 8/2018 campaigns than during the autumn. During the autumn 10/2018 campaign, almost all BVOC emission rates were less than in the earlier campaigns (Figs. 2 and S3).

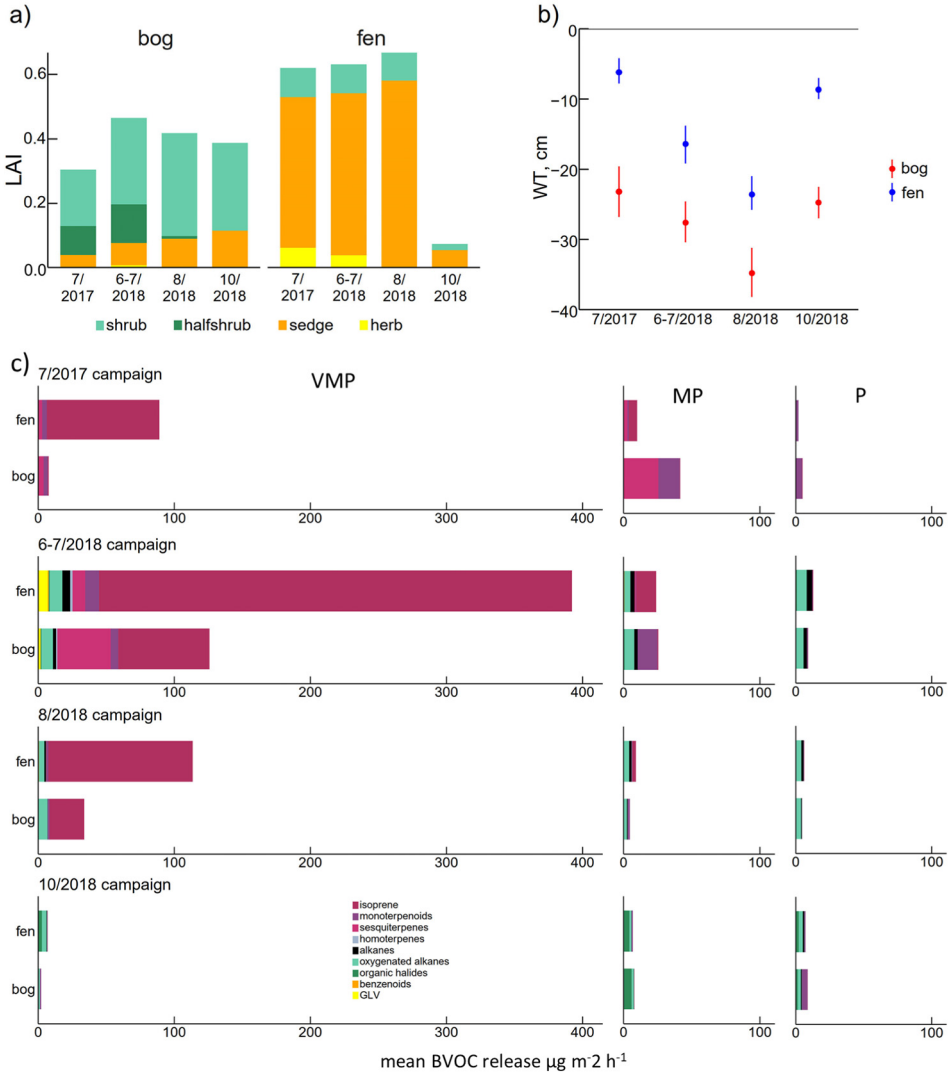

Fig. 1. a) Leaf area index (LAI), b) mean water table (WT) and the 95 % confidence interval, and c) total biogenic volatile organic compound (BVOC) emissions measured during the four measurement campaigns in the growing seasons in 2017 and 2018 in Siikaneva bog and fen sites. Total BVOC emissions are shown separately for intact vegetation (Vascular + Moss + Peat = VMP), moss and peat (Moss + Peat = MP) and bare peat (Peat = P) plots. (c). Variation in BVOC emissions among replicates can be seen as 95 % confidence intervals for each campaign and treatment in the Supplementary material Fig. S2. Note: different standards were used for monoterpenoids and sesquiterpenes in BVOC quantification in the 7/2017 campaign resulting in partly different compounds quantified, and thus this campaign cannot be fully compared to the 2018 campaigns.

3.3. BVOC emissions from the fen and bog sites

BVOC emission rates differed between the two sites (Fig. 1, Table 2). From VMP plots with intact vegetation the total BVOC emission was higher in the fen site (mean: 166.3 µg m^{-2} h^{-1}) than in the bog site (mean: 44.5 µg m^{-2} h^{-1}) (effect of site*treatment interaction on total BVOC emissions: DF = 2, 24; p = 0.0124). The difference was related to the higher isoprene and alkane emissions in the fen (Fig. S3, Tables 3 and S1). For sesquiterpene emission rates, the site effect depended on the campaign as sesquiterpene emissions were higher in the bog than in the fen during the 7/2017 campaign (Fig. S3). There were no differences between sites with regard to the emissions of the other BVOC groups (Fig. S3). However,

Table 2
Multivariate generalized linear model results of the effects of campaign (C), site (S), treatment (T) and their interactions on the overall composition of biogenic volatile organic carbon (BVOC) emissions. The test was conducted for nine detected BVOC groups (see group-specific univariate statistics in Table 3) and for 45 detected BVOC compounds (compound-specific univariate results in Table S2). The test of groups includes data from years 2017 and 2018, whereas the test on the individual compound level only includes emissions in the year 2018.

	Campaign (C)		Site (S)		Treatment (T)		C × S		C × T		S × T		C × S × T	
	$Dev_{3,78}$	p	$Dev_{1,77}$	p	$Dev_{2,75}$	p	$Dev_{3,72}$	p	$Dev_{6,66}$	p	$Dev_{2,64}$	p	$Dev_{6,64}$	p
BVOC groups	205.08	0.001	17.19	0.032	71.72	0.001	22.49	0.118	54.59	0.004	30.29	0.027	51.99	0.002
	Campaign (C)		Site (S)		Treatment (T)		C × S		C × T		S × T		C × S × T	
	$Dev_{2,79}$	p	$Dev_{1,78}$	p	$Dev_{2,76}$	p	$Dev_{2,74}$	p	$Dev_{4,70}$	p	$Dev_{2,68}$	p	$Dev_{4,64}$	p
Individual compounds	761.98	0.001	174.91	0.001	271.08	0.001	271.92	0.001	276.12	0.001	125.59	0.007	108.20	0.002

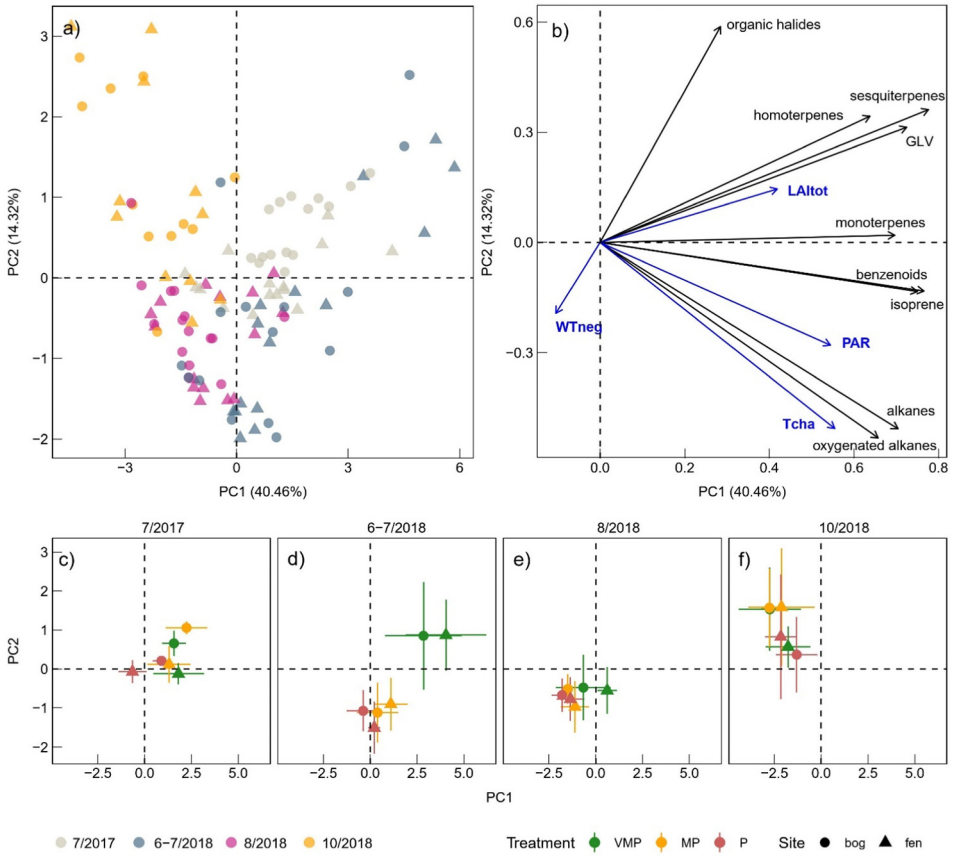

Fig. 2. a–b) Principal components analysis of biogenic volatile organic compound (BVOC) group emissions (black vectors) measured in Siikaneva fen (triangle) and bog (circle) in 2017 and 2018 and c–f) the treatment differences on each campaign. The principal component analysis (PC) is based on the log-transformed emissions of the nine BVOC groups. In frame b, blue vectors represent increase in the total leaf area index (LAItot), temperature in the chamber (Tcha), and photosynthetically active radiation (PAR). The vector WTneg shows the direction of decreasing water table, i.e., distance of WT from the surface. Frames c-f show mean ± standard deviation separately for the treatments (VMP = Vascular + Moss + Peat, MP = moss and peat, P = bare peat) in the different measurement campaigns.

at the compound-level, the alkanes n-nonane, n-dodecane, n-tridecane and n-tetradecane were more abundant in the fen site (Table S2).

3.4. Role of vegetation in BVOC regulation

Vegetation abundance and composition appeared to be a key driver of BVOC emissions (Figs. 3 and S3, Table S1). Isoprene, monoterpenoid, sesquiterpene, homoterpene, and GLV emission rates correlated positively with seasonally varying LAI_{TOT} (Figs. 2 and 3). While isoprene and sesquiterpenes exhibited a strong positive correlation with LAI_{sedge}, monoterpenoids and homoterpenes were related to LAI_{shrub} (Fig. 3). Green leaf volatile emission rates correlated positively with all the different LAI parameters, and thus were not linked to any specific plant functional type (Fig. 3).

Impact of the vegetation removal treatments was evident at the BVOC group level in both sites. In the fen, emission rates in the VMP plots were 13 and 23 times higher than in the MP and P plots, and 2–4 times higher than in the bog, respectively (Fig. 1). The decrease in BVOC emission rates that resulted from the removal of the vascular plants was particularly evident during the 6–7/2018 and 8/2018 campaigns, close to the maximum LAI. In the final campaign (10/2018), when temperatures were low and LAI substantially reduced, vegetation removal had little impact on emission rates (Figs. 1 and 2). The higher BVOC emissions in the VMP plots mainly consisted of isoprene, sesquiterpene, homoterpenes (E-DMNT), and GLV (Fig. S3). Monoterpenoid emissions from the VMP plots were higher than from the P plots GLV were almost exclusively emitted from intact vegetation, except for 1-hexanol found once from two MP

Table 3
Univariate test results of the effects of campaign (C), site (S), treatment (T) and their interactions on the abundance of the nine biogenic volatile organic carbon (BVOC) groups in 2017 and 2018. Statistically significant results are shown in bold text. GLV denotes green leaf volatiles.

	Campaign (C)		Site (S)		Treatment (T)		C × S		C × T		S × T		C × S × T	
	$Dev_{3,78}$	p	$Dev_{1,77}$	p	$Dev_{2,75}$	p	$Dev_{3,72}$	p	$Dev_{6,66}$	p	$Dev_{2,64}$	p	$Dev_{6,64}$	p
Isoprene	**26.11**	**0.001**	3.76	0.071	**8.22**	**0.015**	**7.28**	**0.043**	**22.93**	**0.001**	4.09	0.173	**7.63**	**0.039**
Monoterpenoids	**4.14**	**0.040**	0.27	0.517	**6.02**	**0.010**	0.98	0.551	5.97	0.178	3.95	0.140	5.40	0.343
Sesquiterpenes	**12.61**	**0.004**	**2.95**	**0.047**	**23.75**	**0.001**	1.46	0.205	1.72	0.215	**6.33**	**0.035**	0.00	0.408
Homoterpenes	**6.98**	**0.041**	0.95	0.346	**12.33**	**0.003**	**7.32**	**0.041**	**5.87**	**0.034**	0.00	0.752	0.00	0.509
Alkanes	**63.57**	**0.001**	**8.14**	**0.006**	2.13	0.298	5.08	0.057	**13.04**	**0.006**	1.69	0.343	**14.51**	**0.003**
Oxygenated alkanes	**14.98**	**0.001**	0.01	0.925	0.25	0.732	0.04	0.964	0.32	0.938	1.53	0.170	5.79	**0.021**
Organic halides	**39.03**	**0.001**	0.06	0.772	0.50	0.732	0.04	0.849	0.89	0.650	1.03	0.650	0.20	0.958
Benzenoids	**27.17**	**0.001**	0.76	0.445	0.08	0.974	0.01	0.996	3.16	0.735	6.64	0.112	**18.46**	**0.005**
GLV	**10.48**	**0.008**	0.31	0.557	18.44	**0.001**	0.27	0.667	0.69	0.498	5.03	0.079	0.00	0.762

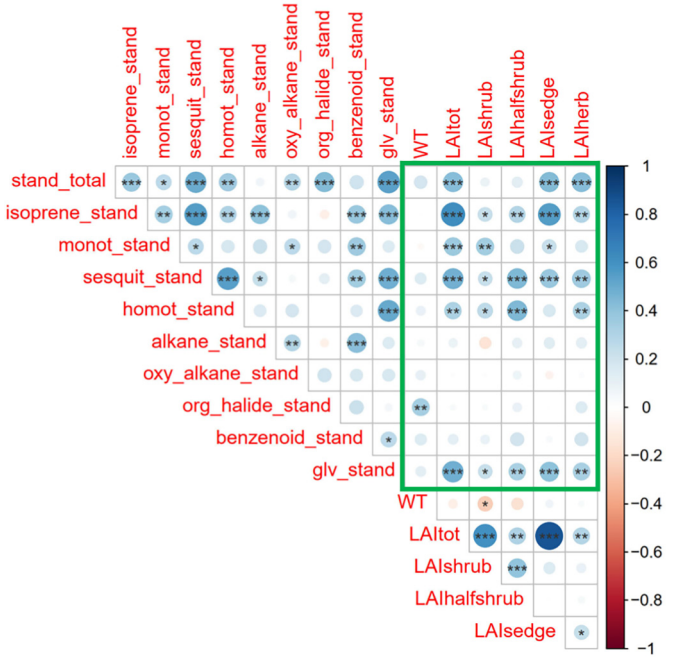

Fig. 3. Correlations of standardized biogenic volatile organic compound (BVOC) group emissions (T = 20 °C and PPFD = 1000 μmol m^{-2} s^{-1} for isoprene; T = 20 °C for the other groups) with environmental factors measured in the Siikaneva fen and bog sites in 2017–2018. Anderson's log-transformation was used on the standardized group emissions. Correlations are shown for isoprene (isoprene_stand), monoterpenoids (mont_stand), sesquiterpenes (sesquit_stand), alkanes (alkane_stand), oxygenated alkanes (oxy_alkane_stand), organic halides (org_halide_stand), benzenoids (benzenoid_stand), green leaf volatiles (glv_stand) and total BVOC emissions (stand_total) with environmental factors: water table (WT), total leaf area index (LAItot), and leaf area index of dwarf shrubs (LAIshrub), half shrubs (LAIhalfshrub), sedges (LAIsedge) and herbs (LAIherb). Stars denote the correlation significance level (***$p < 0.001$, **$p < 0.01$, *$p < 0.05$).

plots of the fen site. Emissions from the MP and P plots were not dominated by any specific compound group. Vegetation had no effect on the emissions of oxygenated alkanes, organic halides and benzenoids (Fig. S3, Table S1).

The impact of the treatments was found also at the compound-level (Tables S1 and S2). In general, 56 compounds were identified from the VMP plots with intact vegetation, 46 compounds from the MP plots, and 41 compounds from the P plots. All compounds, except for four (namely 2,4-dimethylpentane, isooctane, camphor, and terpinene-4-ol), were detected from the VMP plots. Alkanes 2,4-dimethylpentane and isooctane were only found at the fen site, the former from the MP and P plots, and the latter from a P plot. Monoterpenoids (camphor and terpinen-4-ol) were detected only once, from the P and MP plots in the bog site. The sesquiterpene beta-caryophyllene and the monoterpenoid beta-pinene were emitted from all treatments but were most abundant in the VMP plots (Table S2). All other compounds were more sporadically emitted from the different treatments (Tables S1 and S2).

3.5. Impact of drought period in 2018

The effect of drought period in 2018 with lowest WT (Fig. 2) was observed on the emissions of organic halides that were totally absent during the dry 8/2018 campaign (Figs. 3 and S3, Table S1).

3.6. Net BVOC uptake

Total net BVOC uptake ranged from −0.0 to −48.6 μg m^{-2} h^{-1} with the mean −5.4 μg m^{-2} h^{-1}. The significant difference between the measurement campaigns (DF = 3, 36; p = 0.0013) was due to the smaller net uptake during the 7–6/2018 campaign than in the 8/2018 and 10/2018 campaigns (Fig. S2). There were no significant differences in total net BVOC uptake between other campaigns, measurement sites or treatments. Organic halides contributed 81.5 % to the total net uptake consisting mainly of net uptake of dichloromethane. The net uptake was higher than the total net dichloromethane emission (mean net uptake −4.4 μg m^{-2} h^{-1} and mean net emission 0.3 μg m^{-2} h^{-1}). Net uptake of different oxygenated alkanes and alkanes contributed 14.2 % and 3.7 %, respectively. Otherwise, net uptake of monoterpenoids alpha-pinene, beta-pinene, beta-myrcene, 3-carene, and limonene, as well as benzenoids, homoterpenes, sesquiterpenes and isoprene were detected only once or twice.

4. Discussion

Here, we compared the emissions from two adjacent peatlands with differing vegetation composition and explored the impact of vegetation with a plant removal experiment. Our results demonstrate that, in addition to weather conditions, vegetation plays a key role in controlling the quantity and quality of BVOC emissions. Our approach, which included a sedge and a shrub dominated peatland sites and the occurrence of the exceptionally warm and dry period in 2018, also allows us to discuss how the predicted changes in abiotic factors and the associated change in vegetation are likely to alter emissions and their climate impact.

4.1. Diversity of emissions

In line with previous studies (e.g., Janson et al., 1999; Seco et al., 2020) isoprene was the most abundant compound emitted from both sites, accounting for 90 % of total emissions in the fen and 55 % in the bog. Our mean flux values (e.g. 85.1 μg m^{-2} h^{-1} from intact vegetation) were in the same range as other studies (Hellén et al., 2006; Lindwall et al., 2016; Hellén et al., 2020) while the highest standardized isoprene emission rate of 978.6 μg m^{-2} h^{-1} (T = 30 °C and PPFD = 1000 μmol m^{-2} s^{-1} was higher than reported previously from the Siikaneva fen (Haapanala et al., 2006) and from other peatlands (Janson and De Serves, 1998; Tiiva et al., 2007b, 2009; Seco et al., 2020), except for the studies of Tiiva et al. (2007b) and Holst et al. (2010) who reported even higher isoprene emission potentials. The second largest compound groups, monoterpenoids and sesquiterpenes, had similar emission rates than found in previous studies (Faubert et al., 2010b, 2011; Lindwall et al., 2016; Hellén et al., 2020). In addition, we found numerous other BVOCs, some of which have also been reported previously in peatland studies (e.g., octane, hexadecane, nonanal and chloroform) (Rinnan et al., 2005; Haapanala et al., 2006; Hellén et al., 2006; Faubert et al., 2010b, 2011). Furthermore, we did not measure the short-chained BVOCs (<C_5), some of which are highly volatile, in this study, but their emission rates from a peatland ecosystem have been previously quantified with a different method and shown to be substantial (Seco et al., 2020).

4.2. Seasonality in emissions

In this study, peatland BVOC emission rates and composition showed strong seasonality. As the isoprene emission rate is dependent on light and temperature (Guenther et al., 1993) it typically shows seasonality (Tiiva et al., 2007a). For other BVOCs often one or both of these factors play(s) a role in regulating their emissions as well (e.g., Guenther et al., 1993; Kesselmeier and Staudt, 1999; Peñuelas and Llusià, 2001; Tarvainen et al., 2005; Duhl et al., 2008). In our study, total BVOC emissions increased concomitant with an increase in temperature. Accordingly, emissions of all BVOC groups were highest in the end of June or in July, during the peak growing season in northern Fennoscandia. Correspondingly, all BVOC emissions, except organic halides, were at their minimum during the 10/2018 campaign when the temperature was lowest, and when most of the vegetation had senesced.

4.3. Role of vegetation in emission rates and quality

Vegetation type and quantity appeared to be the main controllers of the quality of BVOC emissions. The higher total BVOC emission rates in the Siikaneva fen VMP plots (dominated by sedges) compared to the bog VMP plots (dominated by dwarf shrubs) was a consequence of higher isoprene and alkane emissions in the former. The strong positive correlation between isoprene emissions and sedge leaf area is in agreement with the significant isoprene emissions previously measured from sedges, such as *E. vaginatum*, *E. angustifolium* and *C. rostrata* (Tiiva et al., 2007a; Ekberg et al., 2009). While *E. vaginatum* is found in both sites in Siikaneva, *C. rostrata* and other *Carex* species are characteristic of the fen site. Similarly, the positive correlation between monoterpenoid emission rates and the leaf area of dwarf shrubs found in our study agrees with the established link between woody dwarf shrubs and monoterpenoid emissions (Isebrands et al., 1999; Rinnan et al., 2005). While this suggests that dwarf shrub dominated bogs can potentially have higher monoterpenoid emissions than sedge dominated fens, monoterpenoid emissions from the bog were not significantly higher than the fen site in this study. However, the rather wet bog site studied here contains a relatively low abundance of dwarf shrubs compared to some other bogs (Vasander, 1982; Moore et al., 2002), and hence potentially lower monoterpenoid emission rates.

Using the vegetation removal experiment with intact vegetation (VMP), plots with mosses and peat (MP) and bare peat plots (P), we could link isoprene, sesquiterpene, homoterpene (E-DMNT) and GLV emissions to vegetation. Our results agree with a laboratory experiment that showed over 90 % decrease in isoprene emissions when all vegetation or only vascular plants were removed from ombrotrophic hummock microcosms (Tiiva et al., 2009; Faubert et al., 2010b). However, our results disagree with a previous study in the Siikaneva fen that suggested *Sphagnum* mosses are the main emission source of isoprene (Hellén et al., 2006). Our study, consisting of more replicates and a clustering of vegetation removal treatments, shows higher isoprene emissions in the VMP plots compared to the MP plots in three of the four measurement campaigns, which indicates that vascular plants also have an important role in isoprene exchange in a peatland ecosystem.

In the present study, more monoterpenoids were emitted from the VMP plots than from the P plots agreeing with Faubert et al. (2010b). Furthermore, our finding that the emission rates of alkanes, oxygenated alkanes, organic halides and benzenoids did not differ between the VMP, MP and P plots also agrees with Faubert et al. (2010b) who reported that vegetation removal had no impact on the other BVOCs grouped together. This would suggest that many compounds are emitted in the same abundance from peat and mosses as from vascular plants.

In line with our expectations, GLV were mostly detected alongside vascular vegetation. As the name suggests these compounds are typically found in green leaves of almost all plants – and in line with this, GLV emissions correlated positively with the leaf area of vascular plants. The GLV group are often released as a response to both biotic and abiotic stress (Ameye et al., 2018) such as mechanical damage to plant cells, mostly due to herbivory (Holopainen et al., 2017). In our study, we did not monitor herbivory or pathogenic activity, and thus cannot determine a direct relationship. Mechanical damage to the plants could have been induced during experimental manipulation or during the measurement campaign, although this risk was minimized by undertaking vegetation removal a year before the start of the first campaign and by the removal of newly grown leaves at least a couple of days before each measurement campaign.

4.4. Effects of a warm and dry period

Of note, WT correlated positively with organic halide emissions. Organic halides were present before and after the driest campaign period (the 8/2018 campaign when the water level was deepest at both sites), but not during it. This result supports previous findings that water level drawdown decreases BVOC emissions from peatlands (Tiiva et al., 2009; Faubert et al., 2010b) and changes the BVOC emission mixture (Faubert et al., 2011). Earlier dry spells have been shown to alter BVOC emissions from soil, lichens, and mosses (e.g., Asensio et al., 2007; Edtbauer et al., 2021). Here, we show that mosses and peat-associated microbes of boreal peatlands also respond to drought stress seen as a shift in the composition of BVOC emissions. However, this requires further studies as in here microbial activity was not directly measured.

4.5. Net BVOC uptake

We found that the reactive BVOCs do not directly add up from P to MP and further from MP to VMP. This suggests that vegetation could also consume or trap some of the BVOCs emitted by the peat or mosses. In line with this, we also detected negative net fluxes that indicated BVOC uptake, particularly towards the end of the growing season 2018. Exchange of BVOCs between vegetation and microbes is highly likely as previous studies report bidirectional fluxes (Seco et al., 2007; Holst et al., 2010; Ramirez et al., 2010; Kramshøj et al., 2018; Seco et al., 2020; Baggesen et al., 2021). Recently, soil BVOC uptake by microbial degradation has been suggested to be an omnipresent process (Rinnan and Albers, 2020) but to date, there has been a lack of BVOC consumption studies in peatland soils. For this a proton-transfer-reaction mass spectrometer (PTR-MS) measuring the mixing ratios of BVOCs, would be a better suited method than sampling with adsorbent tubes as in this study.

4.6. Implications of the study

Our study indicates that climate change can directly and indirectly alter the quality and quantity of BVOC emissions from boreal peatlands. In line with earlier studies, the highest total BVOC emission rates at both study sites occurred in the middle of the growing season, simultaneous with maximum leaf area and temperature. This provides additional evidence that the climate change-driven rise in mean temperature and prolonged growing season may increase BVOC emissions from boreal peatlands (IPCC, 2014). However, other changes that co-occur, such as drying trends and the expected vegetation shifts, may challenge the increase in BVOC emissions from boreal peatlands. Currently the combined effect of these concurrent changes hampers our ability to predict BVOC emissions and ascertain the total climate impact of boreal peatlands.

Here, we showed that the drying-associated drop in peatland water table altered the quality of emitted BVOCs. In line with earlier findings of the vital role of water table changes for peatland ecosystem functioning (Mäkiranta et al., 2018; Laine et al., 2019), we found that a deeper water table decreased organic halide emissions. This suggests that the current trend of drying, driven by increased evapotranspiration rates (Helbig et al., 2020) or increased occurrence of extreme climatic events, such as drought periods (Rinne et al., 2020; Zhang et al., 2020) is likely to alter peatland BVOC emissions.

Peatland BVOC emissions could also change with climate-induced changes in plant species composition. Here, we link the emissions of monoterpenoids and GLV to shrub leaf area, and isoprene emissions to sedge leaf area. These dependencies suggest that the climate-induced advancement of shrubs in peatlands is likely to act as feedback to peatland BVOC emissions and, due to the close association between isoprene and sedges, decrease total BVOC release. The observed clear difference in the composition of BVOC emissions between the fen and the bog sites further suggests that the successional transition from minerotrophic fens to ombrotrophic bogs likely impacts BVOC emissions. Such transitions occur even without climatic or anthropogenic pressure due to peat accumulation (Zobel, 1988; Granath et al., 2010; Tuittila et al., 2013) and may be accelerated by hydrological changes (Kokkonen et al., 2019) caused by human-made or natural changes in the catchment area (Tahvanainen, 2011), or driven by increased evapotranspiration (Gorham, 1991; Roulet et al., 1992; Gong et al., 2012). As our study included only one fen and one bog site, multisite studies are needed to truly compare fens and bogs and to understand the dynamic role of vegetation. Furthermore, teasing apart the direct and indirect impacts of climate change (induced warming

and drying) on peatland BVOC emissions requires experimental studies that control water level drawdown and associated vegetation succession.

Changes in BVOC quality and quantity are likely to affect the climate impact of boreal peatlands. In the atmosphere, BVOCs affect SOA formation, atmospheric oxidant concentration (OH and ozone) and, as such, the atmospheric lifetime of methane (Hoffmann et al., 1997; Atkinson, 2000; Kaplan et al., 2006; Virtanen et al., 2010). The effect of changing BVOC emissions on SOA production does not only depend on changes in the quantity of the emissions, but also on their quality as different BVOCs can result in very different SOA yields. For example, long-chained homoterpenes with several C═C bonds are more susceptible to fragmentation during the oxidation process than cyclic monoterpenes (Faiola et al., 2019), thereby leading to lower SOA yields. In addition, isoprene can suppress the SOA yield derived from monoterpenes by reducing the yield of low-volatility products of monoterpene oxidation that would otherwise form SOA (McFiggans et al., 2019). Hence also the observed changes in the quality of boreal peatland BVOC emissions need to be accounted for predicting changes in SOA formation and climate forcing.

CRediT authorship contribution statement

Elisa Männistö: Conceptualization, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization, Funding acquisition. **Henni Ylänne:** Formal analysis, Writing – review & editing, Visualization. **Mari Losoi:** Methodology, Resources, Writing – review & editing. **Markku Keinänen:** Methodology, Resources, Writing – review & editing. **Pasi Yli-Pirilä:** Methodology, Resources, Writing – review & editing. **Aino Korrensalo:** Writing – review & editing. **Jaana Bäck:** Resources, Writing – review & editing. **Heidi Hellén:** Resources, Writing – review & editing. **Annele Virtanen:** Conceptualization, Writing – review & editing, Supervision. **Eeva-Stiina Tuittila:** Conceptualization, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Data availability

Data will be made available on request.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.159809.

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